

Oral Incubation in the Cichlid Fish *Geophagus jurupari* Heckel

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(Plate I)

HISTORICAL RÉSUMÉ

ALTHOUGH reproductive habits of the cichlid fishes assigned to the genus *Geophagus* were described as early as 1855, 1863 and 1865, our knowledge of them has remained, to this day, in a state of disconcerting confusion.

In 1855 Castelnau described how his new species, *Geophagus (Chromys) lapidifera*, carried pebbles in its mouth to form a nest in which the eggs were laid (Pellegrin, 1903). In 1862 the Reverend J. C. Fletcher and Sr. Henrique Antonii collected specimens of one or two species of *Geophagus* that had eggs or young in their mouths (Putnam, 1863; Fletcher & Kidder, 1866). In 1865 Louis Agassiz also obtained a species of *Geophagus* in the mouth of which eggs and young in various stages of development were found (Agassiz, 1865), and within a year he had discovered additional species in a similar condition (Agassiz, 1866; Agassiz & Agassiz, 1868.)² The seeds of confusion, however, were already sown by these pioneers. Agassiz never identified or described his fishes in any detail, and some 14 bottles of unidentified *Geophagus* from the Thayer Expedition to Brazil, the one on which Professor Agassiz collected his fish, are stored at the Museum of Comparative Zoology.

Similar limitations afflict most subsequent observations on the group. Too often one cannot be certain of the identity of the fish concerned. Pellegrin (1903) recognized 17 species of *Geophagus*, while Regan (1906) accepted 12. Of these, three or four appear to have become

generally known. viz. *Geophagus brasiliensis* (Quoy & Gaimard), *G. jurupari* Heckel, *G. surinamensis* (Bloch) and perhaps *G. gymnogynys* Hensel, but one would be hard put to explain the different reproductive habits that have been ascribed to each of them except on the basis of misidentification of the form under observation. Without the background of a much needed taxonomic revision of the genus, as well as an attempt critically to identify each fish in question, it would be pointless to list the observations of all the amateur and professional workers who have described their reproductive behavior. Our purposes will be served by a brief consensus, with mention of the most important papers and the most notable exceptions.

At least ten different accounts of the breeding of *Geophagus brasiliensis* in captivity agree that the eggs and young are cared for by both parents in typical cichlid fashion. Hensel (1870), however, described how a specimen in nature took young into its mouth when disturbed and how these were found crowded into its mouth after the fish had been killed or stunned by a shot.³ Adloff (1922) similarly reported that he had seen the young of a freshly caught *G. brasiliensis* flee into the mouth of the parent several times. Von Ihering (1883, 1920) and Brüning (1931) stated that this species was a mouthbreeder, but their opinions appear to be based on the observations of others. None of these authors mentioned the sex of the fish involved. Guimarães (1930) says nothing about oral incubation in his description of the reproductive habits of this species, both in aquaria and in nature.

Similarly, at least six aquarists have agreed

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² These five publications appear to be the first to mention oral incubation in the cichlid fishes.

³ The fish was said to belong to Hensel's newly described species, *Geophagus scymnophilus* sp. nov., which Pellegrin (1903) and Regan (1906) have both synonymized with *G. brasiliensis*.

that *Geophagus gymnogenys* reproduces itself in typical cichlid fashion, but Haseman (1911a, b), who declared that a subspecies of *G. brasiliensis* was not a mouthbreeder, attempted to catch a female *G. gymnogenys* which was surrounded by small fish. These disappeared into her mouth and reappeared later. When the fish was finally caught, her mouth was full of young. On another occasion, a recently captured specimen of his released young from its mouth.

Although two aquarists have mentioned no signs of oral incubation in their breeding pairs of *Geophagus surinamensis*, Eigenmann (1912) collected a wild specimen carrying young, Beebe & Tee-Van (1922) two specimens similarly encumbered,⁴ and Puyo (1949) two females with eggs in their mouths. Eigenmann (1912) also found a specimen of *G. jurupari* that was sheltering young, while Beebe & Tee-Van (1922) caught two fish of the same species that, following capture, spewed out 58 young between them. Another fish was found to have taken up some 60 young with which it had been placed in an aquarium five days previously, the fish apparently being parent and offspring that had become separated at the time of capture.⁴ Professional ichthyologists and home aquarium fanciers are less at odds with regard to *G. jurupari*; Härtel (1936) and Dvoskin (1955) have described how the female orally incubated both eggs and young in aquaria. Leitholf (1917), however, did not notice any mouthbreeding behavior in his breeding pair of this species.

Among the less well known species of *Geophagus*, Eigenmann (1922) collected a female *G. pellegrini* carrying young. Brüning (1918) described how a male *G. acuticeps* gave shelter to his offspring whenever danger threatened in an aquarium. Two other home aquarium reports on the latter species, however, do not mention mouthbreeding.

Brüning (1918) and Haseman (1911a) erroneously believed that *Geophagus* shelters only the young in its mouth, never the eggs. As to the sex of the incubating parent, what little data there are implicate the female more often than the male, with a single observation that might well indicate that both members of a pair were simultaneously engaged in carrying young (Beebe & Tee-Van, 1922). The statements of Pellegrin (1908) and Miles (1947) that the male typically performs the nursing duties are therefore hard to justify.

⁴ We thank Drs. William Beebe and John Tee-Van for permitting us to use these unpublished data, which were gathered at the station of the Department of Tropical Research, New York Zoological Society, formerly located at Kartabo, British Guiana.

There appears to be no question about the identity of the fish of Eigenmann (1912), Beebe & Tee-Van (1922) and Puyo (1949), but it would be reassuring to check those of Haseman (1911a, b). Our opinion is that *Geophagus jurupari* and *G. surinamensis* are mouthbreeders, while *G. brasiliensis* is not. About the other species we hesitate to commit ourselves. The need for further, more detailed, observations on all species of *Geophagus* is obvious.

PRESENT OBSERVATIONS

The two fish whose behavior is the subject of this paper were kept in standing freshwater aquaria at the home of the senior author for 13 months before their first spawning. At that time the male was about five and one-half inches in total length, the female slightly more than five. About five months previously, the first signs of sexual dimorphism had appeared, accompanied by aggressive behavior on the part of the male. Most notable were the more pointed extension of the posterior rays of the male's dorsal fin and the much more conspicuous elongation of the anterior rays of his pelvics (Plate I). It was the latter outgrowth that seemed to indicate that the fish belonged to the species *Geophagus acuticeps* Heckel (Reid, 1956), but Dr. George S. Myers has recently examined the two fish and found that they belong to the species *G. jurupari* (Register Number, Stanford University, SU 49836).

Ten spawnings have been recorded (Table 1), but the bulk of the observations were made during three of them (Nos. I, III and IV). Details of methods of care and feeding are given in Reid (1956, 1957). Since the senior author was unable to make systematic observations throughout the day or at regular times on successive days, the data do not lend themselves to quantitative treatment. Nevertheless, sufficient time was devoted to observing the activities of the fish to reveal the general pattern of reproductive behavior as well as a number of interesting details.

Typical sequence of events.—Both male and female clean the surface on which the eggs are to be laid, within a few hours of spawning. The spawning act itself does not differ from that of many cichlids, the female laying many small batches of adhesive eggs, each batch being fertilized, in sequence, by the male. The eggs are guarded by both parents. Roughly 24 hours after laying, the eggs are picked up and orally incubated, by both parents or by the female alone. Although our observations cannot be considered conclusive on this point, we believe that the eggs

TABLE 1. SUCCESSIVE SPAWNINGS OF A PAIR OF *Geophagus jurupari* HECKEL

No.	Date 1955-1956	Time	Place ¹	No. Eggs (approx.)	Behavior	Outcome
I	March 5	Morning?	Flat, red shale, 2½x1½ inches	150	Both parents cooperated in care of eggs and young	All young eventually lost, by seventeenth day
II	April 19 or 20	?	?	?	Female alone at time of spawning	Swallowed eggs on fifth or sixth day
III	May 10 ²	9:15-10:45 A.M.	Flat, red shale, 2¼x1½ inches	?	Both parents guarded eggs; female carried them	Swallowed eggs (or young?) on fourth day
IV	May 24	Daytime	Flat, red shale, 2¼x2¾ inches	200	Both parents cooperated in care of eggs and young	Parental care ceased on or shortly before forty-first day; 105 young remained
V	July 9 or 10	?	?	?	Female carried eggs	Swallowed eggs
VI	July 26	Daytime	?	?	Female alone during spawning, separated from male by pane of glass	Eggs eaten on second day
VII	October 6	About noon	Flat, green shale, 1½x1½ inches; few on gravel	350	Both parents cooperated in care of eggs	Swallowed eggs on third day
VIII	November 1	11:20 A.M. —?	Flat, red shale, 2x1¼-2¾ inches; few on gravel	275- 325	Female carried eggs; separated from male on second day	Swallowed brood on eighth day
IX	November 29	Morning	Large piece shale	?	Both parents guarded eggs, which were removed on second day	Artificial incubation unsuccessful, although eggs hatched in two to three days at 81°F.
X	April 24	?	Three small pieces shale, one green, two red, as well as gravel	?		Eggs eaten

FOOTNOTES TO TABLE 1

¹ The first spawning occurred in a 20-gallon home aquarium, 24 × 12 × 16 (high) inches; subsequent spawnings took place in one of similar capacity, 30 × 12 × 12 inches. The former was a community tank, while in the latter the *Geophagus* were maintained alone with the infrequent exception of a small catfish or two.

² On May 3, the female seemed to have eggs in her mouth, but no signs of a nest or other eggs could be found, and subsequent events yielded no clue as to whether a spawning had actually taken place.

are not released from the mouth. On the other hand, one- or two-day-old young are released into depressions dug in the bottom and may be transferred back and forth between the pair. Sometimes the male, sometimes the female, and most frequently both sexes carry the brood. Free-swimming young are released (undoubtedly to feed), and they return to the mouth, and are gathered up by the parents as well, at times of disturbance and at night. Parental care may be exercised for as long as 37 days.

Selection and preparation of spawning site.—Selection of the nest site may be a function of the male, but our data provide only a suggestion that this is so. On the first spawning (I), the male tugged at the stone on which the eggs had been laid, as if attempting to move it. This occurred when the senior author had inadvertently disturbed the fish. At one time (April 24), when the male was being kept in a community tank without his mate, he dug a deep depression in the gravel and attacked the senior author's hand when it was put into the water. Five days before a spawning (III), the male was seen to drag a piece of shale across the tank for about 25 inches, and on the day of the event (III), he dragged another stone to the front of the tank, this stone being the object that both fish subsequently cleaned and used as a spawning place.

Cleaning of the spawning site immediately preceded the false "runs" in which the female engaged just prior to actual egg laying (III). First the pair cleaned the flat stone with their mouths, then they covered it with gravel and again cleaned it off with their mouths. They repeated this procedure over and over, perhaps as a means of thoroughly cleansing the future egg site.

It is possible that this behavior is related to the fact that on four occasions (I, III, IV and VII), a sprinkling of gravel was found on the eggs during part of the time they remained at the spawning site. Härtel (1936) stated that a few hours after spawning, his pair of *G. jurupari* had covered their eggs entirely with sand.

Oviposition and fertilization.—Eggs were laid during daylight hours—so far as definitely known, during the forenoon or early afternoon (Table 1). On two occasions (III and VIII), spawning was observed. On the first, the female swam over the stone several times, her extended ovipositor touching it. After each false "run," she unsuccessfully attempted to drive the male toward the stone. When she began to lay her eggs, in closely packed rows, the male followed, fertilizing each row in turn. On the second occasion (VIII), the male harried the female while she was laying the

eggs by nipping her. The female in turn attacked the male after laying each row, giving him little opportunity to fertilize the eggs. When he followed close behind her, he was able to pass over the newly laid row, but this occurred only once in every five or six rows laid.

Guarding the eggs.—On four occasions when the behavior of the fish was observed during the late afternoon or evening of the day on which the eggs were laid (III, IV, VIII and IX), the female alone guarded the eggs, keeping the male away. Once (VII) it appeared that both might have been so engaged with the female closer and more attentive to the spawn. On the first spawning, it is not known how long the eggs had been laid before they were discovered, but it was the protective behavior of both parents that led to their detection; they attacked the siphon introduced into the aquarium by the senior author. (On the basis of the schedule of events of other spawnings, it is extremely likely that the eggs had been laid that morning).

On another occasion (III), the female was guarding and vigorously fanning the eggs with her pectoral fins and keeping her mate away, when some methylene blue was added to the tank. The male immediately approached the eggs and both parents then guarded them. Later the female again chased the male away. On still another occasion (IX), the female was guarding the eggs on the day of spawning, when water and chemicals were added to the tank. During this operation, both fish guarded the spawn, but the next morning the female alone was doing so.

From this and other behavior to be described subsequently, we conclude that the male would have cared for the eggs from the start, had the female permitted him to do so. On the evening of one spawning day (IV), the female was guarding the eggs alone, but the male persisted in his attempts to take part in this activity. As the male came near the spawn, the female tried to block his approach with her body, but as he became more aggressive, he was able to get past her and settle at the opposite side of the stone. Each time this happened, she chased him away, and he then swam about the bank, foraging through the gravel (displacement activity?) and sometimes returning to the spawn. After a while, the female began to tolerate the male's presence; they then assumed a head-to-head position, lips almost touching while they both fanned the eggs. The following morning they were still fanning in the same position, but later on they began to chase each other, circling about and nipping each other's tail. While guarding the spawn (I) in a community tank, which contained

two *Pterophyllum*, two *Helostoma*, four *Corydoras*, four *Gymnocorymbus* and two loricariid catfish, the parents took positions at opposite corners of the rectangular stone, facing in. When one parent changed position to ward off a potential threat, the other changed position accordingly so that both were continuously guarding the spawn. They first thrust themselves at the intruding fish, and if necessary, they placed their bodies directly between the eggs and the intruder. Finally they would vigorously chase the intruder, although they never actually left the spawn to follow a retreating fish. Their teamwork appeared highly efficient.

Picking up the eggs.—The eggs were picked up during the day after spawning in all instances where observations were made covering this phase (I, III, IV, VII and VIII). The actual performance was seen but once (VII). At 1:00 P.M. both parents began to pick up the eggs in their mouths. While one was so engaged, the other swam about the tank, rolling eggs in its mouth. The fish took turns, picking up only a few eggs at a time, and the procedure required about three hours. Occasionally the two circled about, chasing each other. Both sexes carried eggs after two other spawnings (I and IV), but the female alone gave evidence of having eggs in her mouth during another (III), and during one spawning (VIII) it was impossible to determine whether or not the male ever carried any eggs. On at least some occasions, all of the eggs were not picked up; 50 were left unattended in spawning I, 2 in spawning III, and 45 in spawning IV.

Eggs that were artificially incubated at 81° Fahrenheit hatched in somewhat less than three days. During the course of the present observations, the temperature ranged from 80° to 84° F. These fish have never been observed to spit out unhatched eggs, but Dvoskin (1955) reported that his female regularly did so as late as ten days after spawning. In the light of the above observations, as well as the senior author's experience in confusing with eggs some recently hatched young which had been released from their parents' mouths for the first time, because the young were immobile and their tails practically invisible, we conclude that Dvoskin's fish was manipulating young, not eggs.

Incubation of young.—The young fish were first seen outside the parents' mouths on the sixth (I) and on the eighth (IV) days. The temperature in both cases had been about 84° F. In the latter instance the young were further developed, although still not free-swimming. In both cases the tiny fish were released into a depression dug

in the sand, but in the latter each parent simultaneously used a different depression. The female, who had the greater part of the brood, tried to keep the male away, but he managed to pick up a few strays from her complement.

The young always spent the night in the mouths of their parents. Even as long as 37 days after spawning (IV), when the bulk of the brood was too great to be thus accommodated, the parents appeared to carry as many young as they could at night. The amount of light influenced the activity of the parents and whether or not they released or carried their brood. Often the morning opening of the blinds of the room in which their tank was kept was followed by swimming activity by the parents and then the release of the young into a dish-shaped depression, 5-6 inches in diameter and 1½ inches deep at the center. On the other hand, during the day bright light on either tank (I and IV), seemed to make the parent fish exceedingly wary, and for this reason the electric lights immediately above the tank were usually kept off during daylight hours. Putting on the room lights at night rarely brought about the release of the young, however.

Frequently the initial release of the young was not a simple matter but consisted of ejecting and retrieving the small fish several times, sometimes as rapidly as possible. This might continue for a minute or more before the young would finally be permitted to remain outside. The young were usually more active when first released and the parents had greater difficulty keeping them together, but whether the above-described parental behavior was solely the result of a stimulus-response situation, we cannot say.

Either one or both parents incubated the young. In the first spawning, when the number of young soon became reduced to about 50, there were times when one or the other would carry the whole brood for a day or more while the unencumbered fish swam about and ate. They alternated fairly regularly. In a later spawning (IV), with more than twice as many young to care for, both male and female carried some young every day, although they did not necessarily share the burden equally. If any choice could be made, the female was the more assiduous in orally incubating the offspring. We have already seen that what little information was previously known about this species, as well as other orally incubating species of *Geophagus*, indicates that the female performs the duty with greater frequency than the male.

As the young fish became older, they spent less and less time in their parents' mouths until finally they remained free except in times of disturbance and at night.

The orientation or exact location of the young inside the parent fish was never discerned, but they might be expelled through the mouth or operculi or all three openings at the same time. The female was noted to employ all these methods, while the male rarely released his young except by way of the mouth. The young emerged from under the operculi head or tail first, seemingly at random.

Feeding of parents and young.—Unlike all other orally incubating cichlids known to us, *G. jurupari* takes in food while in the act of carrying young. The pair under observation fed on and off during the entire period of parental care except the three or four days that the eggs were being incubated, but even during this interval the female was observed to suck in tubificid worms while rolling eggs about in her mouth (II and VIII). Considerable numbers of worms were taken on five successive days in the latter case, but in the former, worms were seen to be taken but once, and then they were ejected through the operculi shortly afterward. Both sexes were seen eating while guarding the eggs, after spawning and before they were picked up. The taking of food with young in the mouth was first noted five days (I) and six days (IV) after the day of spawning. In the former instance, which was the first occasion that the young had been seen outside the parental mouth, the female was observed to suck in tubificid worms during the process of picking up the small fish. In the latter instance, the female took in tubificid worms on the day before the young were first seen. Following that occasion, both sexes gingerly took some blood worms after they had picked up all of their brood. Other instances of similar behavior were also noted.

Whether this combined feeding and oral incubation was for the purpose of nourishing parent or offspring is not known. In several instances, the food taken in was obviously too large for the young fish to engulf. Frequently when the young were expelled, a few tubificid worms were also ejected. These were picked up and swallowed while the young were outside the mouth. It is possible that the parents did not swallow any worms when there were young in their mouths, but "saved" them for moments like these. On the other hand, the fish appeared to possess fine powers of oral discrimination between fry and other small objects. For example, on the sixteenth day after spawning (I), each parent was observed to engulf a young fish while in the process of eating daphnia, but the small fish soon emerged through the gill openings. Once the male was observed to pick up a few

fry and then take a little gravel into his mouth and commence chewing movements. After a minute, a few fry and some of the gravel were ejected through the gills and the remainder were spit out (one month after spawning IV).

The observations of Härtel (1936) are in some ways similar to the present ones: "On the fourteenth day a few of the young appeared through the gill openings; they could not swim and were immediately picked up by the mother. Accidentally, I saw the female with a bunch of mosquito larvae in her mouth; she crushed them against the side of the tank and inhaled the 'juice.' The following day encytrae were fed. They were at once taken by the female, chewed and, when she believed herself to be unobserved, ejected in a cloud together with the young. I could see the latter feeding in the cloud." The observations of Dvoskin (1955), on the other hand, are strikingly different. The female carried the brood, and for about ten days she did not eat. The male then began to chew mouthfuls of worms which he spat out in the direction of his mate. She took this into her mouth, presumably to feed the young there.

In the pair observed by us, the most vigorous feeding was performed by either parent while the other was engaged in caring for the entire brood, and the division of labor seemed to be fairly equal. From about the twelfth day after spawning (I and IV) on, the young frequently swam into the cloud of detritus and sediment that the adult fish passed out by their gills during their grubbing on the bottom. (As in all the *Geophagus* known to us and as they had done since their earliest days, the adults frequently took a mouthful of gravel and after chewing it, presumably to extract food, expelled the material through their gill openings and mouth). At first it could not be seen whether the fry were eating or not, but later this was definitely seen to be the case. Since the parents sometimes sifted through the gravel at places in the aquarium far from the young, there did not seem to be any special behavioral mechanism to insure the feeding of the young in the above fashion, but rather a satisfying of the needs of the one by the unmodified self-satisfying behavior of the other.

Return of young to the mouth.—The return of the young *G. jurupari* to the parental mouth definitely results from the interaction of the behavior of both parents and offspring. During the earlier stages of development, the parents, rather than the young, seemed to initiate the return, and since the young could not swim when first released, the parents perforce had to accomplish the deed alone. At this time they did so with

an inhaling, vacuum-cleaner action, and even though the young might be blown back out through the mouth or through the opercular openings, the handling of the fry appeared to be a gentle procedure.

Roughly eight to ten days after spawning (I and IV), the young had become active although they were still not able to maintain themselves indefinitely in mid-water. They usually seemed hardest to control when released for the first time in the morning. The parents were kept busy picking them up as they spread out over the bottom of the aquarium. After a while, the young turned toward the parent fish and began swimming about their heads trying to get back into the oral cavity, or even the gill chambers. Usually the parents picked up the young leisurely, over a period of five to twenty seconds, but if there was any danger, real or no, they were able to secure all the fry within about two seconds. The parents then tilted their heads toward the young, opened wide their mouths, and in a state of high excitement with all fins spread wide, they sucked in the young. The fry also cooperated by swimming to their mouths. Ordinarily the male and female kept their ventral fins close to their bodies while standing guard over the brood, but their pectorals were constantly moving as they apparently fanned (or signaled?) the young. Occasionally when the nearer parent rose a bit in the water, the young also rose in a swarm with it. When one parent moved away to ward off an intruding fish, the young did not follow it, but moved closer to the other parent. On the basis of our observations, however, we are unable to state whether any particular action on the part of the parents served to "call" the young or whether it was an assemblage of visual, and perhaps auditory or mechanical, stimuli that was responsible.

During the later stages, the young usually seemed to make the moves initiating a pick-up. They streamed like a swarm of bees toward the mouth of the nearer parent, who did not always take them in. Whether this behavior was the result of some action on the part of the parent fish or of some other stimulus is not known. On several occasions the parents were seen to refuse to open their mouths even though the young persistently swam about their heads. (It might also be noted that as late as 34 days after spawning (IV), the young still tried to gain ingress through the operculi, although they were never seen to enter either parent by these openings). If the parent fish closed its mouth while there were still a few stragglers outside, these would keep swimming about the head until taken in or until their sibs were released.

One anatomical structure whose role in the picking-up process needs elucidation is the oral valve. This was seen to vibrate rapidly while fry were being returned to the oral cavity.⁵

Cooperation between parents.—That female and male cooperated in cleaning the egg site, guarding the newly laid eggs and orally incubating eggs and young has already been indicated. Coordinated efforts in guarding their brood were naturally more apparent during the course of spawning I, which took place in a community aquarium. We have already noted (p. 80) how effective was the teamwork the pair displayed in guarding the eggs in this situation. As mentioned before, either one or both parents might carry the brood, but as the young grew, it became impossible for a single fish to encompass all of them. Exchange of young took place by means of a depression dug in the gravel into which the young were ejected and from which they were picked up. While the brood was being carried about, the parents did not pay any attention to the other fishes in the aquarium, but when they were about to release the fry they drove all fishes away from the depression they were to use, before ejecting any young. For example, on the morning of the eighth day after spawning I, the male spit all the fry into the depression and the female joined him in picking them up. The male then spit his out again, and while the female was picking them up, he patrolled the area, warding off intruders and picking up any strays missed by the female. Again and again he returned strays to the depression, where they were picked up by the female. After the female had been carrying all the fry for a few minutes, she blew them out through her gills and the male again helped her pick them up. The female then took up the young and ejected them several more times, while the male stood guard, rolling his complement about in his mouth.

As in guarding the eggs, the cooperation between parents was remarkably well developed. When one parent was tending the young alone, the other sometimes seemed to ignore its mate and swam about the tank foraging through the gravel. Even while thus engaged, however, the

⁵ Another structure whose relation to the habit of oral incubation needs elucidation is the pharyngeal gland. The presence of a pair of papillae or compressed lobes on the first branchial arch is considered a generic characteristic of *Geophagus* (Pellegrin, 1903; Regan, 1906). Pellegrin believed it most likely that these structures served some purpose connected with mouth-breeding, and Shaw & Aronson (1954) presented certain additional evidence supporting this view. At least one member of the genus, however, *G. brasiliensis*, does not seem to be an oral incubator.

fish appeared to keep a wary eye homeward. If the tending parent had to rise from the fry to ward off an intruder, the free-swimming parent immediately dashed back to the young.

On one occasion (18 days after spawning IV), each parent fish appeared to be leading a separate group of fry about the entire aquarium. At that time there were about 140 young. Whether such a splitting up of the brood would ever occur under natural conditions is hard to say.

Breakdown of parent-young relationship.—On two occasions events culminating in the termination of the parent-offspring bond were witnessed. On the seventeenth morning after spawning I, there were seven fry left and when they were expelled they immediately tried to return to the parents' mouths. They practically bounced back in as if they were on rubberbands. The parents then began to pick up and expel the young rapidly. One of the fry became injured and began to spiral around. The male picked it up several times, but when it stopped moving he ignored it. The remaining six then began dashing about the tank out of control. Two were eaten by other fishes, and the parents vigorously chased the last four, who showed no response but fled as any small fish might while trying to escape a large one. In a short time all the young had disappeared. The parents roamed the tank apparently searching for them and while doing so they grabbed and tugged at plants in a haphazard fashion.

One month after spawning IV, the more than one hundred young were seen swimming about the aquarium obviously not under the immediate supervision of their parents. When an attempt was made to net some of them, however, both parents hastily picked up the brood in the usual way. The following day it was noted that the parents seemed unable to close their mouths completely when carrying the young. They swam about with their mouths partly open, rhythmically opening them wider in breathing. Three days later the male did not pick up his share of the young even when disturbed with a catching-bell that was carefully manipulated near him in order to remove ten fry from the aquarium. Instead, he retreated toward the bottom and the young nestled about him. Later the same evening, however, he did pick up almost all of the small fish not already being carried by his mate. On the evening of the following day the male was seen to refuse entry to some of the young, continuing to feed on daphnia that had just been put into the aquarium. The next night the male attempted to pick up his share of the brood when the senior author approached the aquarium, but he ap-

peared physically unable to do so. The young remaining outside persistently swam about his head, and he soon released those inside his mouth. Both parents were seen with their mouths crammed with young at midnight, but there were still quite a few others gathered in small groups throughout the aquarium. Four days later, after dark, neither parent was found to be carrying any young, which instead were scattered about the aquarium. Some daphnia were fed, and both parents and young commenced to feed on them. When the female approached one of the small fish, she quickly pursued it and the youngster fled from her. The male, on the other hand, paid no attention to his offspring, nor did they seem afraid of him. Adults and young were kept together for four more days during which the small fish generally stayed away from their parents, occasionally fleeing from them, but sometimes they swam directly in front of their mouths or under their bellies without being molested.

Härtel (1936) also recorded an unusually long period of parental care, more than 30 days, and Schreitmüller (1936b) called attention to the sharp contrast between this and the other, shorter periods exhibited by other cichlids.

Recognition of young by parents.—As noted above, the pair of *G. jurupari* under observation did not eat any young, even after all ties with them had seemingly been broken. In fact, at no time were these specimens seen to attempt to eat any kind of small fish. Although eggs or young might be swallowed early in the sequence of reproductive events (Table 1), the young were never, to the best of our knowledge, eaten later on. The adults were well fed at all times on non-living, dry or wet prepared foods, as well as live tubificid worms, chironomid larvae (blood worms), daphnia, cut-up earthworms, brine shrimp and "mikroworms." On at least three occasions it was noted that dead fry were ignored, not eaten, and that dying fry might either be ignored or repeatedly picked up until they ceased moving.

In order to test the parents' reactions to small, strange fish, two six-day-old black mollies (*Mollienesia*) were put into the aquarium on the twenty-eighth day after spawning (IV). No attention was paid to them, and they were removed after a few days. Four days previous to this, a young fish from the same brood—which had been raised in a separate aquarium with three others like it for 18 days—was returned to its parents' aquarium. This young fish was at the time considerably larger than those being raised by the

parents.⁶ It seemed frightened and stayed motionless near a rock. When the female finally saw it, she swam toward it. The youngster fled to a corner, as if to hide. The senior author then chased it out toward the group of young being tended by the parent fish. The parents were excited by this action and they picked up all of the fry. When the male spotted the lone small fish, he went after it, his mouth full of young. It appeared obvious that his intention was to pick up the newcomer. By evening the small fish was still in hiding and was removed.

DISCUSSION

Many cichlids, belonging to nearly a score of genera, are known to practice oral incubation. Nevertheless, the patterns of reproductive behavior shown by the species that have been studied in sufficient detail may be separated into three major types (Table 2). Two of these groups are represented by a single species—although a few close relatives, not yet well enough known, should undoubtedly be grouped there also—while the bulk of the cichlid oral incubators seem to belong to the third group. Outstanding differences among these three types involve the sex of the principal parent incubating eggs and young, the length of time elapsing before the eggs are picked up and orally incubated, and whether the young ever return to the parental mouth after being released for the first time. That these differences are correlated functionally remains to be seen. We believe it possible that some of the features of oral incubation peculiar to *Geophagus jurupari* are associated with young that are provided with relatively little yolk, as compared with other orally incubating cichlids, and which therefore must begin feeding soon after hatching. Young *G. jurupari* are less well developed at the time of first release than are *Tilapia* and *Haplochromis*, for example, but this fact is at best only indicative of a poor endowment of yolk. A comparative study of eggs and young is needed to help establish this point.

Greenwood (in Lowe, 1957) reported that the period of parental care in *Tilapia leucosticta* extends for about 32 days, which appears to be longer than in any other fish belonging to the third group. Lowe pointed out that the eggs of this species are smaller and more numerous than those of many other African mouthbreeding

⁶ After 27 days in a separate 7½ gallon aquarium (35 days after being spawned), these four young were almost one inch long, while their sibs of the same age being raised by the parent fish were only about half that length.

TABLE 2. COMPARISON OF THREE MAJOR TYPES OF ORAL INCUBATION AMONG CICHLID FISHES¹

Type	Spawning Location	Interval of time from spawning until:			Sex of principal parent: ²		
		First eggs picked up	Hatching from mouth	First release from parental care	Preparing egg site	Carrying eggs	Carrying young
<i>Geophagus jurupari</i>	On flat stones	About 24 hours	About 3 days	About 6-8 days	30-37 days	Male and female, or female	Male and female
<i>Tilapia macrocephala</i>	In depression on bottom	20-130 seconds	6-10 days	8-20 (mean 14) days	8-20 (mean 14) days	Male	Male
<i>Tilapia</i> spp., <i>Haplochromis</i> spp.	In depression or other nest on bottom	From less than one to a few minutes	2½-6 days	4-20 (mode 14) days	10-32 (mode 20) days	Female, or male and female	Female, or male and female

FOOTNOTES TO TABLE 2

¹ The figures are tentative, with the exception of those concerning *T. macrocephala* which are taken from the ample studies of Aronson (1949) and Shaw & Aronson (1954).

² In those species studied in detail, cases in which the opposite sex has been found to perform the duties are usually on record. For example, female *Tilapia macrocephala* and male *Haplochromis multicolor* occasionally orally incubate.

cichlids. Again a correlation between provision of yolk and length of parental care is suggested.

Because of the conflict of reports as to whether the various species of *Geophagus* do or do not practice oral incubation, we at one time entertained the idea that this habit was a direct response to outside interference, or threat of interference, and that this would explain why species known to orally incubate in the wild had not been reported to do so in captivity. The present observations lend no support to this idea; the pair of *G. jurupari* incubated their eggs and young just as assiduously when kept alone as when living in a community aquarium with several good-sized fishes of other species. One difference was apparent, however. The amount of chasing, nipping and other molestation between mates was noticeably greater when the pair bred alone.

Two peculiarities of mouthbreeding in *Geophagus* that may well have misled aquarists are the relatively long delay before the eggs are picked up and the undeveloped state of the young when first liberated (see p. 81).

That *G. jurupari* waits practically a whole day before picking up and orally incubating its spawn, in the meantime guarding and fanning it in typical cichlid fashion, poses the question whether this state of affairs could represent a stage in the evolution of the other two major types of cichlid oral incubation (Table 2). Such a stage is not incompatible with the mode of origin of piscine oral incubation suggested by Darwin (1871), Breder (1933, 1934), Myers (1937), and, in part, Ogilby (1916), but not essential to it. At any rate, it does not appear necessary to consider that the habit of mouthbreeding indicates any phylogenetic relationship between the neotropical genus *Geophagus* and the other, African, genera that contain orally incubating species, because of the probability of multiple origin of this habit within the Family Cichlidae.

We believe that further studies of reproductive behavior in *Geophagus jurupari* and its close relatives would be especially revealing because of the long association of parent and offspring and the relatively undeveloped state at which the young are first released from the mouth, in addition to the sharing of duties by male and female and the evident variability in their feeding behavior during the period of parental care. An extensive program, such as the one Dr. Lester R. Aronson of the American Museum of Natural History in New York has carried out with *Tilapia macrocephala*, is called for, but first of all standardized conditions that result in a high fre-

quency of spawning in *G. jurupari* must be developed. It is unfortunately true that spawning pairs of this species have seldom become established under the prevailing conditions of captivity.

SUMMARY

1. Reports on the reproductive habits of several cichlid fishes assigned to the genus *Geophagus* disagree as to whether or not oral incubation is practiced. On the basis of a review of the literature, it is believed that *G. jurupari* and *G. surinamensis* are mouthbreeders, but that *G. brasiliensis* is not.

2. Extended observations on a breeding pair of *G. jurupari* confirmed its status as an oral incubator.

3. Instead of picking up the eggs soon after spawning, as do other mouthbreeding cichlids, both parents guarded them for about a day before commencing oral incubation. Both sexes or the female alone carried the eggs.

4. The young were given shelter in both parents' mouths for more than thirty days, a much longer period of parental care than is exercised by other mouthbreeding cichlids.

5. Both parents fed through most of the period of parental care, even while in the act of carrying the young and, occasionally, the eggs.

6. The significance of these features in connection with the evolution of oral incubation and the amount of yolk provided for the young is briefly discussed.

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EXPLANATION OF THE PLATE

PLATE I

- FIG. 1. The pair of *Geophagus jurupari* Heckel whose reproductive behavior formed the basis for the present report. The male is on the right. Photographed on October 18, 1955, by S. C. Dunton, Staff Photographer, New York Zoological Society.
- FIG. 2. The male, showing the extensions of the

pelvic (ventral) fins. These continued to grow, and at the time of death, in January, 1958, one had reached approximately the middle of the caudal fin. The other previously had been broken off. Photographed as above.

- FIG. 3. Two of the young from spawning IV. Age, 3½ months. Photographed by S. C. Dunton.